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THE DEVELOPMENT OF A CARBONIFEROUS BRACHIOPOD, *CHONETES GRANULIFER* OWEN

F. C. GREENE

INTRODUCTION

Through the kindness of Professor J. W. Beede the writer had placed at his disposal for study a large collection of *Chonetes granulifer*, the adults alone probably numbering two thousand specimens. The majority of these specimens are finely preserved and this together with the great range in their size, gives an excellent opportunity for a study of the development of the species.

Chonetes granulifer has been found in the following horizons arranged in descending order:

Permian Series	Ft. Riley limestone. Wreford limestone.
Pennsylvanian Series	Neosho shale. Florena shale. Cottonwood limestone. Eskridge shale. Neva limestone. Elmdale formation. Americus limestone. Emporia limestone. Burlingame shale. Howard limestone. Severy shale. Topeka limestone. Deer Creek limestone. Lecompton limestone. Oread limestone. Kickapoo limestone. Stanton limestone.

First will be taken up a study of the form from the Florena shales at Florena and Grand Summit, from which a complete series was obtained, and then a study of the development based on this series. This study has been under the direction of Professors E. R. Cumings and J. W. Beede of Indiana University, and the author wishes to express his deep gratitude for their aid and assistance. The photographs for the plates were also made by Professor Cumings.

Owen's type specimen of *C. granulifer* came from the Carboniferous limestone, near the mouth of Keg Creek, Iowa.[1] This locality has never been definitely correlated with the Kansas section, but as near as can be made out from Meek's discussion of the rocks of the Missouri River section[2] and Owen's description[3] of the locality from which the type specimens were taken, as correlated by Beede and Prosser,[4] it appears to come from some horizon between the Topeka and the Tecumseh limestones, probably nearer the Deer Creek limestone than any other. The material which the writer used, contained specimens covering practically the entire range of the species, including the equivalent of the horizon from which the types were taken.

SPECIFIC CHARACTERS

Mature form.—Shell semi-circular in outline, having the greatest breadth at the hinge-line, with cardinal angles somewhat attenuate. The size of the shell varies greatly. Size of largest specimen, 33 mm in width by 19 mm in length. Average size of adult, 28 mm in width by 15 mm in length. The shape also varies in that the cardinal angles of some specimens are much more mucronate than in others (Plate I) and in some specimens there is a tendency to develop a mesial sinus in the ventral valve. Both of these characters are seen in Plate I, rows 3, 4.

Dorsal valve.—In the Grand Summit specimens (the most perfectly preserved in the lot) the dorsal valve is concave to the extent of two or three mm. This valve is ornamented with radiating striae and concentric lines of growth around the margin. The striae number about fifty near the beak but at the frontal margin increase to about one hundred and fifty by implantation. The shell is punctate in the furrows between the striae. The striae become obscure on approaching the hinge-line. Immediately under the beak, this valve is at first convex, but becomes concave farther forward.

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[1] Owen, *Geol. Rep. Wis., Iowa, and Minn.*, p. 583.

[2] Meek, *U. S. Geol. Surv. Nebr.*

[3] Owen, *Geol. Rep. Wis., Iowa, and Minn.*

[4] Prosser, "Comparison of the Carb. and Penn. Form. of Neb. and Kans.," *Jour. Geol.*, Vol. V, pp. 1–16, 148–72.

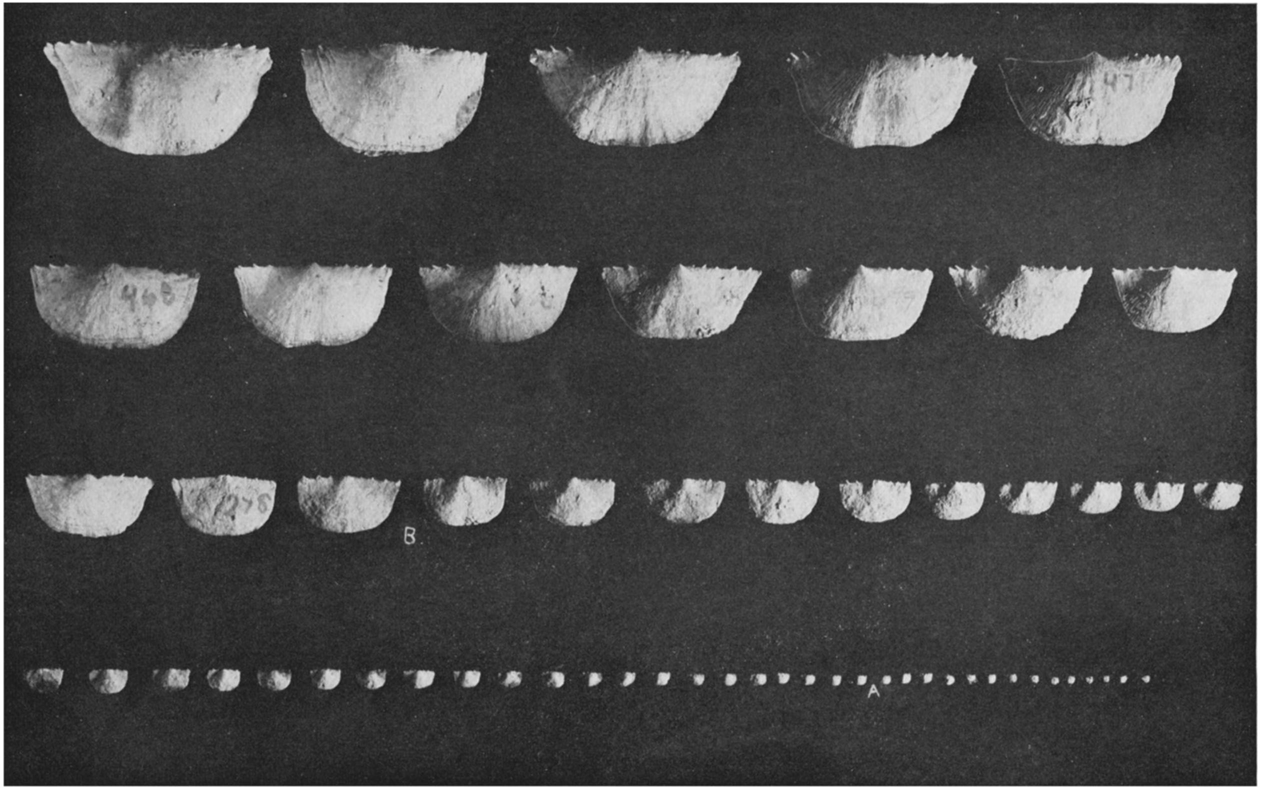
Ventral valve.—The convexity of this valve exceeds the concavity of the dorsal valve to a very great extent in some specimens. In other specimens this valve follows the dorsal valve closely. The striae of this valve are similar to those of the dorsal. Shell punctate in the furrows between the striae. What appear to be large punctae are scattered over the surface of this valve. These are lighter in color than the rest of the surface and are largest at the anterior margin, growing smaller and more thickly set toward the beak. They possibly correspond to the spines of Producti.

The beak projects slightly over the hinge-line. Cardinal area long and narrow; longer than the greatest width of the shell farther forward. It lies at an angle of 45° to the plane of the shell (Plate II, Fig. 12, 13) grooved with horizontal striae; the greater part of the area is on the ventral valve. The hinge areas of the two valves form an obtuse angle.

Two plates of the cardinal process of the opposite valve partially close the delthyrium. The hinge area of this valve is bordered by a row of seven to eleven spines on each side of the beak, growing larger toward the cardinal extremities. This valve is the larger of the two (Plate IV, Fig. 4).

Interior of dorsal valve (Plate II, rows 3, 4).—Convex. Hinge-line straight. The cardinal process is bifid, stands at an angle of 120° with the plane of the valve and is one millimeter in length. On the ventral side of this process is a pit which corresponds to the convexity mentioned just in front of the beak on the exterior of the dorsal valve. From the base of the cardinal process five septal ridges radiate. Two of these pass forward at an angle of 25° or 30° to the hinge-line. They also unite back of the cardinal process to form a little lip over the process. Just back and above them are the two sockets for the hinge teeth.

Two other lateral septa pass forward from the edge of the pit at an angle of 70° with the hinge-line. The fifth ridge is the mesial septum. It is at right angles to the hinge-line and extends forward half the length of the shell. With the other four septa it forms the boundaries of the pit. This pit was probably formed at a very young stage, and


Row IV
Row III
Row II
B
Row I
A

therefore the septa do not extend to the cardinal process as in some of the Productidae. The scars of the adductor muscles lie on each side of the mesial septum, extending over the next ridge. The brachial markings, shown on a few specimens of this valve, are somewhat obscure, and reniform in shape, pointed at the front. They lie on each side of the mesial septum, just within the row of granules marking the limits of the visceral cavity.

This valve is ornamented with granules (from which the species derives its name of *granulifer*). These are largest and most numerous at the forward edge of the visceral cavity, and the mesial sinus, growing fainter and more thinly scattered posterially. At the anterior margin they also grow fainter until they form distinct radiating rows.

Interior of ventral valve.—Very concave. Granules similar to those of dorsal valve, except that instead of having a group of granules on the anterior end of the mesial septum, they are arranged along its sides and help to form the partition between the long, median adductor muscle scars and the subovate diductor muscle scars. Hinge-line straight, with the exception of the delthyrium. There are two teeth on each side of this opening. The deltidium extends to the beak.

Nepionic form—dorsal valve.—Length 1 mm and breadth 1 mm. Longitudinally semi-elliptical in shape; concavity greater than in mature form in proportion to the size. The convexity mentioned as being opposite the beak near the hinge on the dorsal valve of the mature form, is the most prominent feature of this valve of the incipient form. Here it nearly equals the length of the shell and is more elongate than in the adult. Surface without striae.

Nepionic form—ventral valve.—This valve is also without striae. On each extremity of the hinge-line is a spine pointed laterally and posteriorly. The ventral mesial sinus is a regular feature of this valve. A sharply outlined pit also occurs regularly on this valve just anterior to the beak.

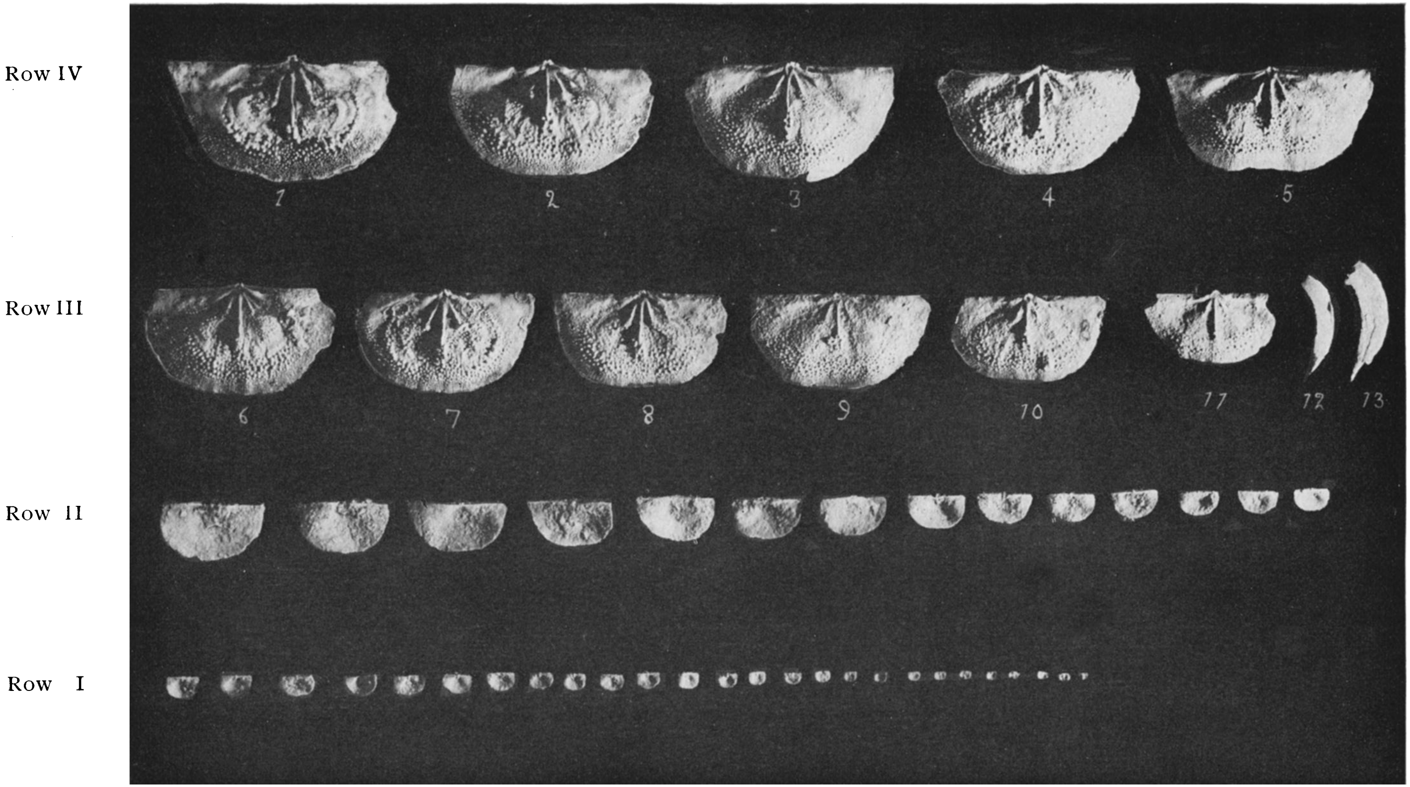
DEVELOPMENTAL CHANGES

The change in shape may be seen from the following table of the measurements of a series of specimens (not the series shown in Plate I).

1. 0.9 mm×1.0 mm
2. 1.0 mm×1.0 mm
3. 1.0 mm×1.0 mm
4. 1.1 mm×1.1 mm
5. 1.2 mm×1.2 mm
6. 1.3 mm×1.2 mm
7. 1.5 mm×1.25 mm
8. 1.5 mm×1.4 mm
9. 1.5 mm×1.2 mm
10. 1.9 mm×1.4 mm
11. 1.9 mm×1.5 mm
12. 2.0 mm×1.5 mm
13. 2.25 mm×1.5 mm
14. 2.25 mm×1.6 mm
15. 2.5 mm×1.75 mm
16. 2.75 mm×1.5 mm
17. 2.8 mm×1.75 mm
18. 3.0 mm×2.0 mm
19. 3.25 mm×2.25 mm
20. 3.5 mm×2.25 mm
21. 4.0 mm×2.4 mm
22. 3.9 mm×2.5 mm
23. 3.9 mm×2.75 mm
24. 4.0 mm×2.5 mm
25. 4.25 mm×2.9 mm
26. 4.6 mm×2.9 mm
27. 4.75 mm×3.25 mm
28. 5.5 mm× 3.5 mm
29. 6.0 mm× 3.5 mm
30. 6.5 mm× 3.5 mm
31. 6.8 mm× 3.9 mm
32. 7.0 mm× 4.0 mm
33. 8.0 mm× 4.0 mm
34. 9.5 mm× 5.5 mm
35. 10.25 mm× 5.5 mm
36. 11.0 mm× 6.0 mm
37. 11.0 mm× 6.5 mm
38. 13.0 mm× 7.0 mm
39. 13.25 mm× 7.5 mm
40. 16.5 mm× 8.0 mm
41. 16.25 mm× 8.5 mm
42. 18.5 mm× 9.5 mm
43. 19.0 mm× 9.5 mm
44. 21.0 mm× 9.5 mm
45. 20.5 mm×10.5 mm
46. 21.0 mm×10.5 mm
47. 22.0 mm×11.5 mm
48. 23.5 mm×12.0 mm
49. 24.5 mm×13.0 mm
50. 28.0 mm×13.0 mm
51. 24.0 mm×14.0 mm
52. 30.0 mm×15.0 mm
53. 33.0 mm×19.0 mm

Ventral valve (*Plate I*).—The mesial sinus in the youngest specimen is a deep, narrow groove near the beak. This occurs regularly up to the 16th specimen, that is, one about 1.6 mm×1.2 mm in size, after which it occurs only at irregular intervals. From the youngest up, it moves forward so that in the older specimens it is seen on the anterior margin. The striae appear distinctly for the first time on the fifteenth specimen (size 1.6 mm×1.1 mm). On the youngest specimens there are two cardinal spines (Plate IV, Figs. 1–3, 6–8) one on each side of the beak. These are located on the extremity of the hinge-line in the youngest specimen, but as the hinge-line becomes longer, the spines are added successively at the extremities. No. 15 in this series shows the first traces of an additional spine, the new spine appearing, of course, between the original spine and the lateral margin. The

PLATE II



number of spines increases about every eighth or ninth specimen, until it reaches the maximum of eleven on one side of the beak, or twenty-two on the entire hinge-line, which was the largest number noticed.

The shape of the youngest specimen is nearly square, while in the oldest the breadth is nearly twice the length. As will be seen by the above table of measurements, this change from one to the other is somewhat irregular.

The angle formed by the hinge-line and the sides of the shell gradually changes from an angle of 90° to a more and more acute angle, although, as has been pointed out before, the angle varies greatly in the adult (Plate I).

Dorsal valve.—The striae do not appear distinctly on this valve until the twenty-fifth specimen, (4.3 mm×2.5 mm) but this is probably due to the fact that some of the earlier stages have been omitted from this series, and that some are incrusted in the concavity or water-worn, which renders the striae invisible in them.

The most notable thing about the developmental changes in this valve concerns the small convexity mentioned in the description of the incipient form. In the smallest specimen this occupies one-half the space of this valve and extends from the hinge-line forward three-quarters of the length of the shell. In the twenty-eighth specimen it is crowded well up under the hinge-line and is so small in comparison to the size of the shell, that it is hardly distinguishable. In the oldest forms, it is so close up under the hinge-line as to be entirely obscured.

Interior of dorsal valve.—In the interior of this valve, the granules in the visceral cavity continually become fewer as the specimens become larger after the beginning of the ephibic stage. The muscular and brachial markings also become stronger as the size increases.

DEVELOPMENT

As a complete series was obtained from the Florena shales at Florena and Grand Summit, this is used as a basis of comparison. A complete series might have been obtained from Florena alone, but as the adults were compressed, Grand Summit specimens were substituted for them.

STAGES IN DEVELOPMENT

As in any series, the division into stages is more or less arbitrary, but there are several factors which determine approximately the different stages. In the series of ventral valves (Plate I, rows 1 and 2) it will be seen that all stages prior to specimen 14 (point *A* in the plate) are not marked with striae and have only the one spine (Plate IV, 1–3, 6–8) while beyond this point the striae appear and increase in number regularly (Plate IV, fig. 5). This point is taken to mark the end of the nepionic and the beginning of the neanic stage. The latter stage continues until the shell takes on its adult characters, such as the number and strength of the striae, the shape of the cardinal angles, a widening of the hinge area causing the beak to project and the hinge to appear bent. The point *B* about marks this division although it cannot be drawn with the same precision as the division between the first two stages.

The last two (and largest) specimens in the series represent the old age or gerontic stage. The intervening specimens represent the adult or ephibic stage.

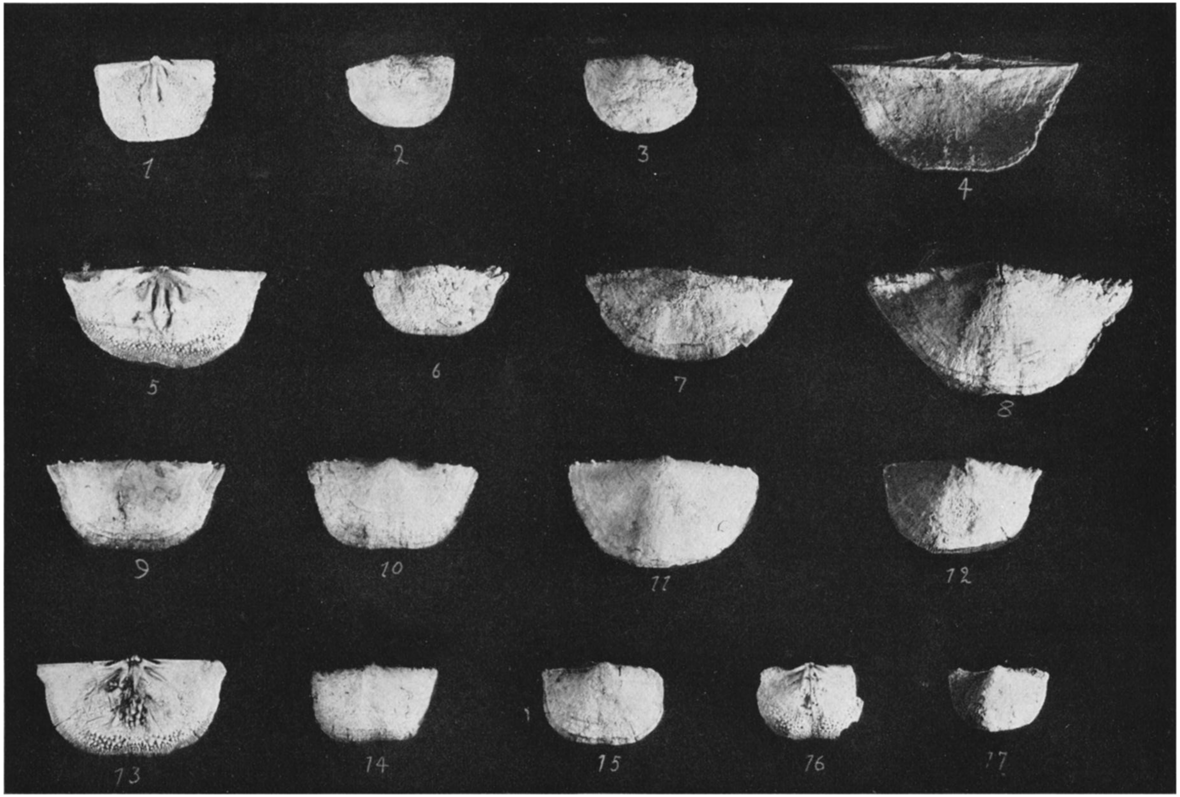
Another series is made to show further the last two stages. This is the series of specimens of the interior of the dorsal valve (Plate II, rows 3 and 4). Here the last specimen represents the gerontic stage. This shows (1) a great thickening of the shell; (2) prominence of the muscular and brachial markings; (3) greater length of hinge-line; (4) a lesser number of granules within the visceral cavity. These characters in this brachiopod are indications of old age.

COMPARISON OF THIS SERIES WITH SPECIMENS OF THE GENUS *CHONETES*, OLDER AND YOUNGER GEOLOGICALLY

It will be noted from the measurements discussed under "Developmental Changes," that the length and breadth of the shell of the nepionic stage are about equal. *This is true of practically all the Silurian and early Devonian species of Chonetes in the adult stages.*

The acceleration in the development of this species is illustrated by the appearance of a pair of spines in the nepionic stage in specimens less than 1 mm in diameter instead of in the neanic stage as in *C. scitulus*, where they first appear on specimens about 2 mm in

PLATE III



diameter.[1] In *C. granulifer* the youngest form obtainable has the spines on the extreme outer edge of the hinge-line.

As mentioned under the description of the Specific Characters in the incipient form of this shell, there is a deep pit or sinus just in front of the beak on the ventral side, and a corresponding convexity just in front of the hinge-line on the dorsal side. This would be an indication of an early species with these characters and also the two preceding. This form is found in the species *Chonetes lepidus* from the Marcellus shale[2] which represents the probable type of shell from which *C. granulifer* is descended.

The figure,[3] which is a ventral view, shows a deep sinus and in the description, it is stated that the dorsal side follows the curves of the ventral. It will be noted that *C. lepidus* is a striated species, while the nepionic stage of *C. granulifer* is glabrous. This has little bearing, as it is a general characteristic of the incipient shells of brachiopods to be glabrous.

Ephibic stage.—Following the laws of development, we could assume the great bulk of adults of *C. granulifer* in the upper Carboniferous of Kansas and below the Florena members of the Garrison formation to be like the ephibic stage in the Florena—Grand Summit series, and upon investigation, this proves to be the case, while above and below these limits, they should be more like the gerontic and late neanic stages respectively. This holds true in nearly every instance.

As was stated in the introduction, the type specimens probably came from a horizon between the Topeka and Tecumseh limestones. Specimens from these horizons correspond with the typical ephibic form, so that the type specimens represent just about the normal form of the species.

We find Norwood and Pratten's species, *C. smithii*,[4] that of Meek and Worthen,[5] and that of Hall and Clark[6] to be a short-eared form with a relatively short hinge-line and the shell longer and narrower than the adult of *C. granulifer* from Grand Summit, and it is found that all these come from a much lower horizon. Thus it will be seen that they correspond to the early ephibic stage of our series. This throws them into the species *C. granulifer* as already done by Schuchert and Weller.

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[1] Raymond, *The Developmental Change in Some Common Devonian Brachiopods*, Vol. XVII, pp. 277–300. Pls. XII–XVIII.

[2] Hall, *Pal. N. Y.*, IV, Pt. 1, pp. 132 and 142, Pl. XXII, Fig. 12.

[3] *Ibid.*

[4] Norwood and Pratten, *Jour. Acad. Nat. Sci. Phil.* (2), Vol. III, p. 24, Pl. II, Figs. 2*a–c*.

[5] Meek and Worthen, *Geol. Surv. Illinois*, Vol. V, 1873, p. 570, Pl. XXV, Fig. 11.

[6] Hall and Clark, *Pal. N. Y.*, VIII, Pt. 1, 1892, XV B, Fig. 12.

Gerontic stage.—In the case of the gerontic form we find the same thing to be true. Meek and Hayden[1] finding a form with mucronate cardinal angles, longer hinge-line, much thicker valves, and, as they say, "the area of its smaller valve ranges more nearly at right angles to the plane of the shell, than in the Illinois species"[2] (*C. smithii*), they called it a new species, although they suspected it of being allied to, or possibly the same species as, *C. smithii.* The above characters are found in the gerontic stage of the Grand Summit specimens, and Meek and Hayden's material was from a higher horizon than the Florena shales. The fact that the area of its smaller valve ranges more nearly at right angles to the plane of the shell than in the Illinois species, is due directly to the fact that it is a gerontic form. One of the characteristics of this stage is the thickening of the shell, especially in the pedicle valve, material being added to the inner surface of the shell. To compensate for this, and keep the visceral cavity its normal size, shell material is added at the hinge-line, which thickens the cardinal area of the pedicle valve and forces the pedicle valve back, making the hinge-line of this valve more nearly at right angles to that of the brachial valve (Plate II, Fig. 12–13).

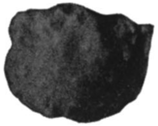
In Prosser's collection from the Neosho (the next horizon above the Florena) near Strong, Kansas, the majority of the specimens exhibit a form remarkably like the gerontic stage in the Grand Summit series.

A collection from the Oread limestone at University Hill, Lawrence, Kans., made by Mr. Chas. D. Ise, bears out the foregoing conclusions to a remarkable degree. The figures (Plate III, Figs. 14–17) show a form identical in shape with the early ephibic stage in the series. The hinge-line is short and the cardinal angle is nearly or quite 90°. There is a tendency in many of the specimens to develop

[1] Meek and Hayden, *Pal. Up. Mo.*, p. 22, Pl. I, Fig. 5 *a–e*.

[2] *Ibid.*

PLATE IV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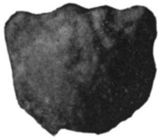
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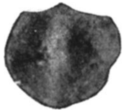
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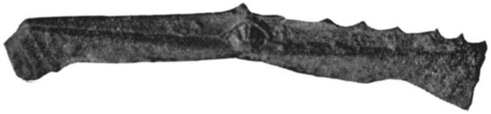
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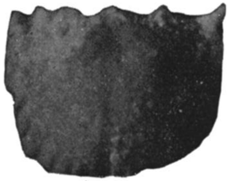
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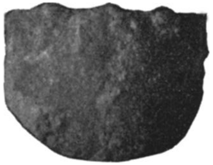
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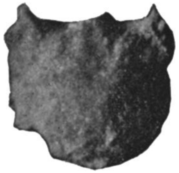
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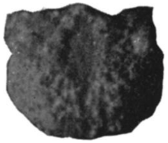
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a comparatively deep sinus. In the interior of the dorsal valve, the granules are arranged around the margin of the visceral cavity alone. The septa are very weak when compared to the later forms.

In the Permian rocks (Ft. Riley limestone) we find that the species has reverted. This form is much smaller, has many granules on the interior, brachial and muscle markings weak, is thin shelled and approaches very nearly in shape to the nepionic stage of *C. granulifer* and therefore the earlier species of the genus. So far as is known, this is the last of the species of *Chonetes* in the Mississippi basin (Plate III, Figs. 1–3).

CONCLUSION

The writer has endeavored to show that, by taking as a basis a series of *Chonetes* from the horizon of the Upper Carboniferous, forms corresponding to the different stages may be found in the rocks above and below this. Thus the nepionic stage represents species from the Silurian and Devonian; the neanic and early ephibic species from the Carboniferous; and the later ephibic and gerontic species from the Upper Carboniferous, while the Permian or last form reverts back again in form to the early species.

EXPLANATION OF PLATES

Plate I.—Series showing ventral view, Florena shales, at Florena and Grand Summit.

Plate II.—Rows 1, 2, Series showing dorsal view, Florena shales, at Florena; cross-section of Grand Summit specimen; cross-section of Prosser's Neosha specimen. Rows 3, 4, Interior of dorsal valves, Florena shales at Florena.

Plate III.—1, Ft. Riley Limestone; 2, Ft. Riley Limestone; 3, Ft. Riley Limestone; 4, Ft. Riley, No. 10, top of Neosho; 5, Neosho, Prosser's Collection; 6, Neosho, Prosser's Collection; 7, Neosho, Prosser's Collection; 8, No. 6 Crusher Hill, bottom of Neosho; 9, Florena at Grand Summit; 10, Florena at Grand Summit; 11, Florena, Ulrich's Quarries near Manhatten, Kan.; 12, Topeka, at Topeka; 13, Topeka, at Topeka; 14, Oread, University Hill, Lawrence, Kan.; 15, Oread, University Hill, Lawrence, Kan.; 16, Oread, University Hill, Lawrence Kan.; 17, Oread, University Hill, Lawrence, Kan.

Plate IV.—1, 2, 3, 5, 6, 7, 8, specimens from the series shown in Plate I, enlarged ×20, to show details of marking ventral vein. 4, hinge area enlarged ×3. Florena shales at Florena.